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# New distributional records of *Celonites tauricus* (Hymenoptera, Vespidae, Masarinae) and new data on its behaviour at flowers

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## Abstract

New records of *Celonites tauricus* Kostylev, 1935 are reported from Chios, Rhodes, Samos (Greece), Dagestan (Russia), Georgia, and the main portion of Azerbaijan (previous records were made from the Nakhchivan Autonomous Republic only). Flower visits of imagines were observed at six species of Lamiaceae, four of them being recorded for the first time as forage plants of *C. tauricus*. The newly recorded *Teucrium canum* Fisch. & C.A. Mey. and *Ziziphora taurica* M. Bieb. (both Lamiaceae) are principal forage plants in Dagestan and the Crimea, correspondingly. The behaviour of females at flowers of *Z. taurica* differs from that previously described at flowers of *Teucrium chamaedrys* L. and *Satureja thymbra* L. (also Lamiaceae) in that pollen removal from the anthers and nectar uptake take place separately from each other in temporal succession. This difference is obviously caused by the flower structure of the genus *Ziziphora*, specifically its much longer corolla tube. Females also try to collect pollen from flowers of *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó but usually without success, while nectar uptake from this species is successful. The specialized morphological structures of the females for pollen-uptake from the nototribic anthers and pollen-transfer from the exoskeleton to the mouthparts are described. They are similar to those of the closely related *Celonites abbreviatus* (Villers, 1789), and consist

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of specialized stiff "knobbed" pollen-collecting setae covering the anterior surface of the head, particularly the frons and the clypeus, as well as comb-like rows of specialized, particularly strong pollen-brushing setae along the anterior margins of the inner surface of the first and the second segments of the fore tarsi. Males of *C. tauricus* patrol in flight along the forage plants of the females. Successful copulations occur either on flowers or on the ground.

**Keywords**
Caucasus, Crimea, mating behaviour, pollen wasps, *Salvia*, trophic relationships, *Teucrium*, *Ziziphora*

## Introduction

With 374 described species (the latest calculation published by Rahmani et al. 2020), the pollen wasps or the subfamily Masarinae *s. l.* (including Gayellinae) are distributed through Mediterranean and temperate to hot semi-arid to arid areas of the world outside the tropics but not further north than 50°N or further south than 50°S (Gess 1996; Gess and Gess 2010). The females of pollen wasps live solitarily and provision their larvae with pollen instead of paralysed insect prey as a protein source (Gess 1996; Gess and Gess 2010; Mauss et al. 2019). This bee-like life form has probably evolved within the stem lineage of the Masarinae (Carpenter 1982, 1988; Mauss 2007), though a recent molecular phylogenetic analysis indicates that it might have evolved independently within the Gayellini and Masarini (Piekarski et al. 2018). Many pollen wasp species are oligolectic, i.e., adapted to collect pollen and nectar from a narrow range of forage plants (Gess 1996; Gess and Gess 2010). Most of them are poorly known and rarely collected insects. These wasps are particularly sensitive to habitat changes due to special requirements to the presence of their forage plants and a suitable nesting site (Gess and Gess 2010).

*Celonites tauricus* Kostylev, 1935 is a species of pollen wasps hitherto known from the Crimea, Kos, Armenia, Nakhchivan Autonomous Republic of Azerbaijan, Turkey, Cyprus, Syria, and Northern Iran (Mauss et al. 2016; Fateryga 2017; Fateryga et al. 2021). Bionomics of *C. tauricus* was studied in the Crimea and in Kos. The species is known to visit nototribic flowers of six species of Lamiaceae of the genera *Satureja* L., *Teucrium* L., *Thymus* L., and *Ziziphora* L. while the primary forage plants are *Teucrium chamaedrys* L. in the Crimea and *Satureja thymbra* L. in Kos. Pollen uptake from such flowers is performed with specialized stiff "knobbed" setae on the frons (Mauss et al. 2016). Nesting of *C. tauricus* is poorly known: only three nests of this species were found in the Crimea. They consisted of one, two, and three cylindrical mud cells attached to the underside of small stones (Mauss et al. 2016).

The purpose of the present contribution is to report new distributional records of *C. tauricus*, as well as new forage plant records, and to describe the behaviour of the imagines at flowers. Specialized pollen-collecting and pollen-brushing structures of the female of *C. tauricus* are also briefly described within the framework of this study.

## Materials and methods

Field observations were carried out in Dagestan in the vicinity of Talgi (Makhachkala urban okrug, 42.876697°N, 47.445123°E, ca. 270 m a.s.l.) on 12.06.2019 and in the Crimea in Lisya Bay (Feodosiya urban okrug, 44.898251°N, 35.157508°E, ca. 25 m a.s.l.) on 07.06.2020 and 10.06.2020. The first locality (Fig. 1A) was an abandoned open mine covered with sparse herbaceous vegetation with solitary shrubs of *Cotinus coggygria* Scop. and *Rhus coriaria* L. (both Anacardiaceae). The most prominent plants in flower were *Cachrys microcarpos* M. Bieb. (Apiaceae), *Teucrium canum* Fisch. & C.A. Mey., *T. chamaedrys* (Lamiaceae), and *Capparis spinosa* var. *herbacea* (Willd.) Fici (Capparaceae). The second locality (Fig. 1B) was a dry stony streambed surrounded with semidesertic dry terraces with solitary trees of *Elaeagnus angustifolia* L. (Elaeagnaceae). Plants in flower were very scarce there; the most numerous one was the annual *Ziziphora taurica* M. Bieb. (Lamiaceae) that occurred within a small spot in the streambed while some other species were sparsely distributed across the terraces.

Wasp activity was observed visually and documented using a Canon EOS M6 camera with a Sigma AF 105 mm f/2.8 macro lens (scale up to 1:1). Flower preferences of the wasps were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the locality. Total investigation time was about two hours in the vicinity of Talgi and about 10 hours in Lisya Bay.

Additional material was examined in museum collections abbreviated as follows: **AMNH** – American Museum of Natural History (New York, USA), **FSCV** – Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia), **MSNVE** – Natural History Museum of Venice (Venice, Italy), **OLML** – Upper Austrian State Museum (Linz, Austria), **ZISP** – Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), **ZMMU** – Zoological Museum of the M.V. Lomonosov Moscow State University (Moscow, Russia), **AF** – collection of A.V. Fateryga (Feodosiya, Russia), **JG** – collection of J. Gusenleitner (Linz, Austria), and **VM** – collection of Volker Mauss (Michelfeld, Germany). Every specimen examined by V. Mauss was labelled with an individual, serial database number (dbM = database Mauss) printed on the determination label.

The species affiliation of the specimens recorded in Dagestan that are lacking the characteristic dark antennal tips of typical *C. tauricus* (Mauss et al. 2016) was proofed by DNA barcoding in addition. Sequencing was accomplished by AIM Advanced Identification Methods GmbH Leipzig following standard methods of DNA extraction from a single female (dbM 5998) collected and stored in 96% pure ethanol, PCR for Cytochrome Oxidase subunit 1 (COI-5P), cycle sequencing of forward and reverse strand and sequence editing. The obtained COI-5P sequence is 286 bp long (BOLD process ID CECYP021-22) and clusters closely together with sequences available for typical specimens of *C. tauricus* from Kos.

SEM micrographs of the wasp structures were taken using a Hitachi SE3500 Scanning Electron Microscope. Two female specimens from Dagestan and one from the

Crimea were studied and compared with a female of *Celonites abbreviatus* (Villers, 1789) from Greece (dbM 2823). The wasp fragments were simply air-dried, mounted on stubs and coated with gold and palladium.

**Figure 1.** Habitats of *Celonites tauricus* Kostylev, 1935 **A** vicinity of Talgi in Dagestan **B** Lisya Bay in the Crimea.

## Results and discussion

### *Celonites tauricus* Kostylev, 1935

*Celonites abbreviatus tauricus* Kostylev, 1935: 108, [♀]. Type locality: "Крым" [Crimea]; neotype (designated by Mauss et al. 2016), ♀ (dbM 4305): Crimea, vicinity of Feodosiya, Lisya Bay, 16.06.2010, A. Fateryga (OLML).

*Celonites spinosus* Gusenleitner, 1966: 359–362, ♀ ♂. Type locality: "Kusadasi" [Turkey]; holotype, ♀ (dbM 4665): Turkey, Kusadasi, 11.06.1964, J. Gusenleitner (JG). Synonymized by Mauss et al. (2016).

*Celonites abbreviatus invitus* Gusenleitner, 1973: 58–59, ♀ ♂. Type locality: "Türkei, Gürün" [Turkey]; holotype, ♀ (dbM 4662): Turkey, Gürün, 05.06.1970, J. Gusenleitner (JG). Synonymized by Mauss et al. (2016).

**Material examined (new records). Greece: Chios:** Spartounta, 38.5428°N, 25.9964°E, 13.06.2007, 1 ♀ (dbM 5353), leg. A. Ebmer [OLML]; W Pyrgi, Kato Fanou, 38.2219°N, 25.9672°E, 12.06.2007, 3 ♀ (dbM 5354–5356), leg. A. Ebmer [OLML]; **Rhodes:** Kolymbia, Akra Vagia, [36.2536°N, 28.1759°E], 29.05.2005, 1 ♂ (dbM 5181), leg. B. Tkalců & O. Tkalců [OLML]; **Samos:** Mt. Kerkis, NE shoulder, [37.7490°N, 26.6406°E], 08.07.1994, 1 ♀ (dbM 5357), leg. A. Ebmer [OLML]; Mt. Kerkis, S shoulder, [37.7182°N, 26.6250°E], 11.07.1994, 4 ♀ (dbM 5358–5361), leg. A. Ebmer [OLML]. **Russia: Dagestan:** [Makhachkala urban okrug], vicinity of Talgi, 42.8767°N, 47.4451°E, 25.06.2018, 1 ♂, leg. Yu. Astafurova, K. Fadeev, V. Loktionov, M. Mokrousov & M. Proshchalykin [AF]; ibid., on *Teucrium canum*, 12.06.2019, 2 ♀, 1 ♂, leg. A. Fateryga [AF], 1 ♀ (dbM 5511), 1 ♂ (dbM 5510), leg. A. Fateryga [VM], 13.06.2021, 1 ♀, leg. A. Fateryga [AF], 18.06.2021, 1 ♀ (dbM 5998, BOLD process ID CECYP021-22), leg. A. Fateryga [VM]; **Crimea:** [Yalta urban okrug], Miskhor, [44.4289°N, 34.0855°E], 01.08.1887, 1 ♀ [ZISP]; Sudak urban okrug, Cape Meganom [44.7940°N, 35.0815°E], 27.05.2016, 1 ♂, leg. A. Fateryga [AF]; ibid., on *Ziziphora taurica*, 27.05.2016, 1 ♀, leg. A. Fateryga [AF]; Feodosiya urban okrug, Lisya Bay, [44.8983°N, 35.1575°E], 22.06.2016, 1 ♂, leg. A. Fateryga [AF]. **Georgia:** Kasbek, [42.6950°N, 44.5147°E], 1 ♀ [ZISP]. **Armenia:** [Armavir Province], Parakar, [40.1665°N, 44.4070°E], 02.05.1925, 1 ♀, [leg. M. Rjabov] [ZMMU, on loan in AMNH]. **Azerbaijan:** [Masally District], Zuvand, [39.0048°N, 48.4771°E], 08.06.1985, 1 ♂, leg. V. Tobias [FSCV]. **Turkey:** Ankara Dikmen, [39.8650°N, 32.8570°E], 05.07.1959, 1 ♀ (dbM 5652), leg. K. Guichard [MSNVE]. **Cyprus:** Ca. 5 km N Lemithou, Pinus-Zone, 34.9689°N, 32.8075°E, 15.06.2013, 1 ♀ (dbM 5348), leg. A. Ebmer [OLML]; Troodos, Mt. Olympos N, Pinus-Zone, 34.9289°N, 32.8703°E, 10.06.2013, 1 ♀ (dbM 5347), leg. A. Ebmer [OLML]; Troodos, Mt. Olympos N, Pinus-Zone, 34.9417°N, 32.8703°E, on *Nepeta troodi*, 11.06.2013, 1 ♀ (dbM 5346), leg. A. Ebmer [OLML]; Mt. Troodos, [34.9234°N, 32.8808°E], 28.06.1937, 1 ♀ (dbM 5622), leg. G. Mavromoustakis [MSNVE]; ibid., 12.08.1948, 1 ♀ (dbM 5620), leg. G. Mavromoustakis [MSNVE]; ibid., 02.08.1965, 1 ♀ (dbM 5621), leg.

G. Mavromoustakis [MSNVE]; Troodos, S of Mt. Olympos, [34.9319°N, 32.8683°E], 07.07.1987, 1 ♀ (dbM 5345), leg. A. Ebmer [OLML]; Troodos, S of Mt. Olympos, Sun Valley, [34.9319°N, 32.8683°E], 10.07.1987, 5 ♀ (dbM 5340–5344), leg. A. Ebmer [OLML]; ibid., 15.07.1987, 2 ♀ (dbM 5338, 5339), leg. A. Ebmer [OLML].

**Distribution.** Greece (Chios, Kos, Rhodes, Samos), Russia (Dagestan, Crimea), Georgia, Armenia, Azerbaijan, Turkey, Cyprus, Syria, Iran. The species is new to Chios, Rhodes, Samos, Dagestan, Georgia, and the main portion of Azerbaijan (previous records were made from the Nakhchivan Autonomous Republic only). The examined specimen from Armenia was reported by Kostylev (1929) as *Celonites abbreviatus*.

**Flower-visiting records.** *Teucrium canum* was the only plant species observed to be visited by males and females of *Celonites tauricus* in Dagestan (Table 1), while they were not recorded on three other species of *Teucrium* flowering at the same locality, namely *Teucrium chamaedrys*, *Teucrium hyrcanum* L. and the species known in the flora of Dagestan (Murtazaliev 2009) as *Teucrium polium* L. "*Teucrium polium*" was previously recorded as a forage plant of *Celonites tauricus* in the Crimea (Mauss et al. 2016), but it has to be noted that there is a taxonomic problem with this plant taxon. True *T. polium* does not occur in Eastern Europe, while the species commonly known there as "*T. polium*" is currently treated as *Teucrium capitatum* L. (Tutin and Wood 1972; Govaerts et al. 2005–2022; Fateryga and Fateryga 2019). On the other hand, the lectotype designated for *T. capitatum* (Rosúa and Navarro 1987) does not correspond very well to "*T. polium*" from Eastern Europe (including Dagestan and the Crimea), and seems to belong to a different taxon.

Specimens of *Celonites tauricus* were observed in the Crimea in 2020 at flowers of five species of Lamiaceae (Table 1). Two of them, that is *Teucrium chamaedrys* and *Thymus tauricus* Klokov & Des.-Shost., were previously recorded as forage plants of this wasp (Mauss et al. 2016), while *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó and two annual species of *Ziziphora* are reported for the first time. The principal forage plant was *Ziziphora taurica* followed by *T. chamaedrys*, while visits to the remaining species were occasional.

The identity of the subspecies of *Salvia nemorosa* L. is also taxonomically complicated. It is generally accepted under the name "*Salvia nemorosa* subsp. *pseudosylvestris* (Stapf) Bornm." (Govaerts et al. 2005–2022; Yena 2012) despite

**Table 1.** Flower-visiting records of females and males of *Celonites tauricus* Kostylev, 1935.

| Plant taxon | Σ sightings of flower-visiting individuals | | | |
|---|---|---|---|---|
| | Dagestan, 2019 | | Crimea, 2020 | |
| | ♀ | ♂ | ♀ | ♂ |
| Lamiaceae | | | | |
| *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó | | | 5 | |
| *Teucrium canum* Fisch. & C.A. Mey. | 3 | 2 | | |
| *Teucrium chamaedrys* L. | | | 13 | 1 |
| *Thymus tauricus* Klokov & Des.-Shost. | | | 3 | |
| *Ziziphora capitata* L. | | | | 1 |
| *Ziziphora taurica* M. Bieb. | | | 25 | 6 |
| Other plant taxa | | | | |

the fact that such a nomenclatural combination was not validly published, because Bornmüller (1907) applied it to a variety *S. nemorosa* β [var.] *pseudosylvestris* (Stapf) Bornm. (as "*pseudo-silvestris*"), not a subspecies.

**Behaviour of females at flowers.** The behaviour of females of *Celonites tauricus* at flowers of *Teucrium canum* in Dagestan was similar to the previously described behaviour of this species at flowers of *Teucrium chamaedrys* in the Crimea and at flowers of *Satureja thymbra* in Kos (Mauss et al. 2016). During these flower visits, the females stood on the lower lip of a flower and took up nectar and pollen simultaneously. The proboscis was protruded deeply into the corolla tube while the female performed rapid back and forth movements of the anterior part of her body, rubbing her head over the nototribic anthers. In this manner pollen grains were removed from the pollen sacs and accumulated on frons and clypeus. Periodically flower visiting was interrupted and the pollen grains were transferred from the frons to the mouthparts by alternating brushing movements of the fore legs and the pollen was being ingested. This pollen-brushing behaviour took place either on flowers or on the ground in the close vicinity of the plants. Similar behaviour was observed in the Crimea in 2020 at flowers of *T. chamaedrys* and *Thymus tauricus*.

The behaviour of females at flowers of *Ziziphora taurica* was different. The behavioural sequence of such a flower visit could be usually subdivided into three phases. During the first phase, a female stood on the lower lip of a flower and performed rapid movements of her head for a very short period (not longer than a second), rubbing its anterior parts over the anthers (Fig. 2A). In the following second phase, the female protruded her proboscis and moved her body headfirst deeply into the corolla tube so that only the posterior half of her body remained visible in outside view. During this phase, the anthers were in contact with the dorsal mesosoma and often also with the first and the second metasomal tergum (Fig. 2B). The duration of the second phase was much longer than the first one; usually it lasted for some seconds. The third phase started, when the female retracted her proboscis and appeared outside the corolla tube again. Then she was rubbing her head over the anthers once more so that pollen accumulated on her frons (Fig. 2C). Subsequently, the female usually performed pollen-brushing behaviour that took place on the same flower. Very often she brushed pollen from her frons while she was standing on the flower and continued to accumulate pollen on her clypeus that was still in contact with the anthers (Fig. 2D). After that, the pollen was brushed from the clypeus to the mouthparts as well (Fig. 2E). When the fore legs were brought between the mouthparts, the pollen was apparently ingested. After the pollen had been brushed from both the frons and the clypeus, the female sometimes repeated the rapid movements of her head, rubbing it over the anthers again, in the same way as in the first phase (Fig. 2F). The duration of the third phase was variable depending on how many times the wasp switched her behaviour from pollen removal from the anthers to brushing the pollen grains from the frons and the clypeus, and back; sometimes this phase was the longest. At regular intervals the females interrupted flower visits and stood on the ground. During this time, they performed alternating grooming movements of the fore legs over the body including the dorsal mesosoma and metasomal terga, covered with pollen grains.

**Figure 2.** Behaviour of females of *Celonites tauricus* Kostylev, 1935 at flowers of *Ziziphora taurica* M. Bieb. in Lisya Bay (details see text).

Thus, the pollen-collecting behaviour of the females of *Celonites tauricus* at flowers of *Ziziphora taurica* differs from that at flowers of *Teucrium*, *Satureja*, and *Thymus* in that pollen removal from the anthers and nectar uptake take place separately from each other in temporal succession. This difference is obviously caused by the flower structure of the genus *Ziziphora*, specifically its much longer corolla tube in comparison with that of the genera *Teucrium*, *Satureja*, and *Thymus*. Therefore, it is impossible for the wasps to reach the nectar with the proboscis and to make contact with the anthers with the frons simultaneously. A behavioural pattern similar to that of *C. tauricus* at flowers of *Z. taurica* is known for *Celonites sibiricus* Gusenleitner, 2007 at flowers of the genus *Dracocephalum* L. (also Lamiaceae) which also have a long corolla tube (Fateryga 2020). The main difference between them is that females of *C. sibiricus* do not return to pollen collection from the same flower after nectar uptake has been finished inside of the corolla tube.

The behaviour of females of *Celonites tauricus* at flowers of *Salvia nemorosa* subsp. *tesquicola* was similar to that at flowers of *Ziziphora taurica* in that the attempts to remove pollen from the anthers and nectar uptake also took place separately from each other in temporal succession. But in contrast, these pollen-collecting attempts by *C. tauricus* at *S. nemorosa* subsp. *tesquicola* usually failed. During the first phase, a female stood on the lower lip of a flower and attempted to rub over the anthers with her frons but usually she actually came into contact with the stigma instead of the anthers (Fig. 3A). During the second phase, the female protruded her proboscis deeply into the corolla tube while she performed rapid back and forth movements of the anterior part of her body, apparently trying to rub her head over the anthers, though the head was in fact not in contact with them (Fig. 3B). However, one female of *C. tauricus* was observed with yellow pollen of *Salvia* on the exoskeleton (well distinguishable from the white pollen of *Ziziphora*, the orange pollen of *Teucrium chamaedrys*, and the lilac pollen of *Thymus tauricus*). This means that at least sometimes the pollen-collecting attempts of *C. tauricus* females at *S. nemorosa* subsp. *tesquicola* are successful. There was no third phase observed at flowers of this species, i.e., the wasps did not return to separate pollen-collecting attempts after nectar uptake. Flower visits to *S. nemorosa* subsp. *tesquicola* occurred only occasionally (Table 1), i.e., this species was not a principal forage plant. Such visits to a suboptimal plant species might be caused by the scarcity of the pollen sources, since they were observed in a locality with very low abundance of flowering plants (see above).

The behaviour of *Celonites tauricus* at flowers of *Salvia nemorosa* subsp. *tesquicola* was somewhat similar to that observed for the closely related *Celonites abbreviatus* at flowers of *Salvia officinalis* L. (Schremmer 1959). In the latter case, the pollen removal from the anthers and nectar uptake also took place separately from each other in temporal succession. But in contrast to the situation in *C. tauricus*, the pollen-collecting attempts by *C. abbreviatus* at *S. officinalis* were always successful.

**Pollen-collecting and pollen-brushing structures.** Examination of a female of *Celonites tauricus* under a SEM revealed that it possesses the same morphological structures for pollen-uptake and pollen-transfer that were previously described in detail for the closely related *Celonites abbreviatus* (Schremmer 1959; Müller 1996). The pollen-

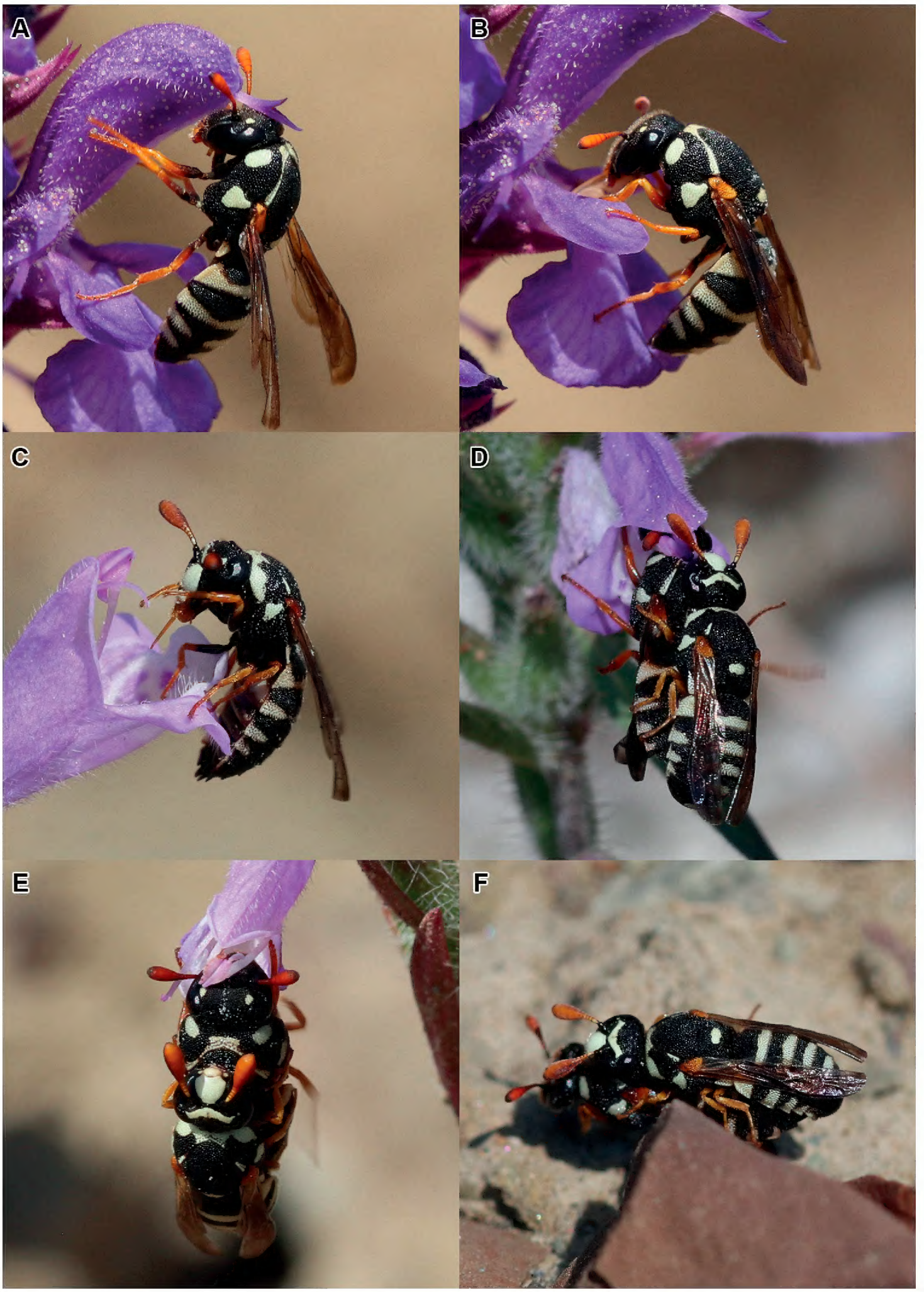


**Figure 3.** Behaviour at flowers and mating of *Celonites tauricus* Kostylev, 1935 in Lisya Bay **A, B** females on flowers of *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó **C** a male on a flower of *Ziziphora taurica* M. Bieb. **D, E** copulation on flowers of *Z. taurica* **F** copulation on the ground.

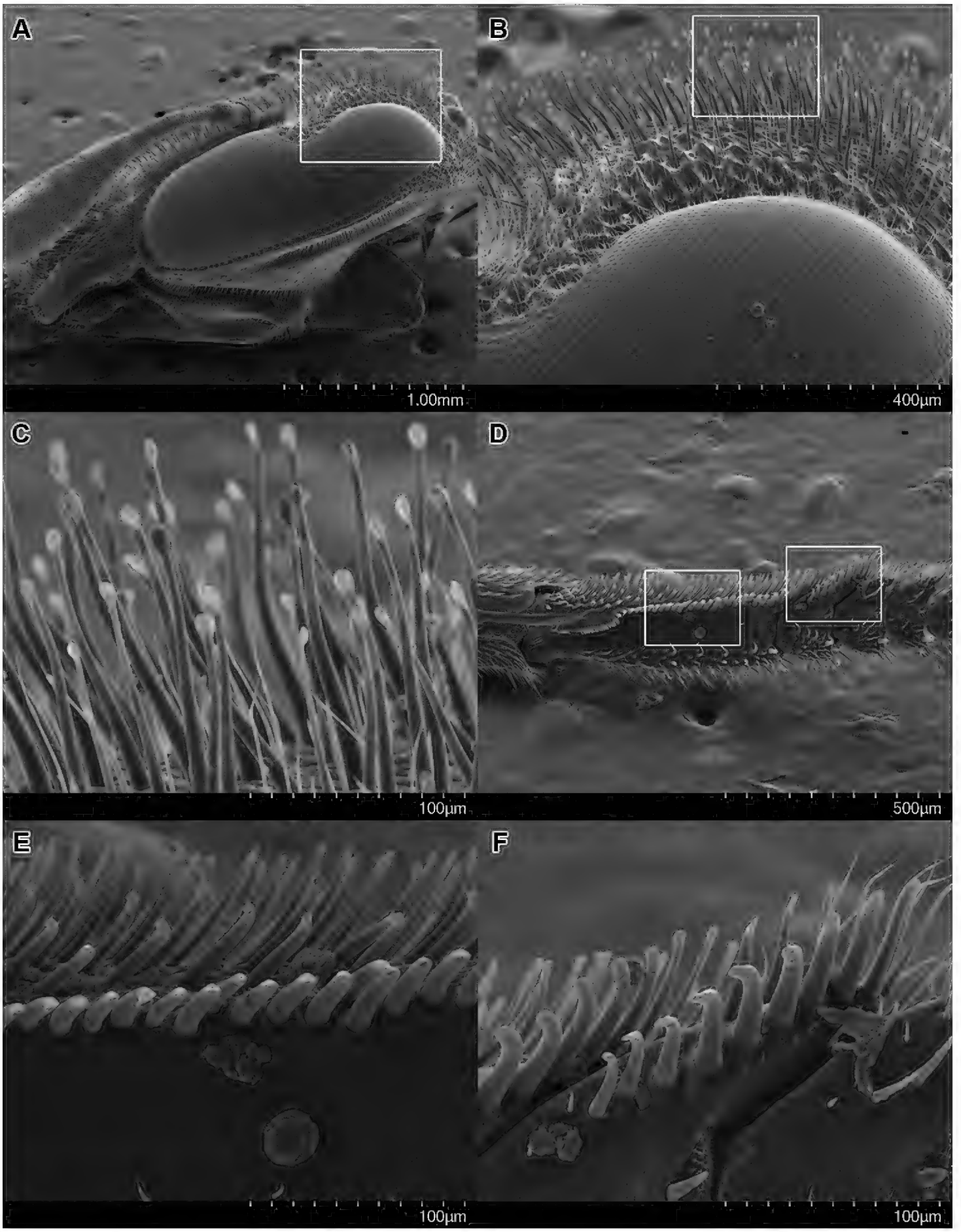


**Figure 4.** SEM micrographs of the pollen-collecting and pollen-brushing structures of a female of *Celonites tauricus* Kostylev, 1935 **A** head in lateral view **B** close up of the frons (marked rectangular area in **A**) showing specialized stiff "knobbed" pollen-collecting setae **C** close up of "knobbed" setae (marked rectangular area in **B**) **D** inner surface of the left fore tarsal segments 1–3 **E** close up of the tarsomere 1 (left marked rectangular area in **D**) showing a comb-like row of specialized, particularly strong pollen-brushing setae along its anterior margin **F** the same for the tarsomere 2 (right marked rectangular area in **D**).

collecting apparatus consists of specialized stiff "knobbed" setae covering the anterior surface of the head, particularly the frons and the clypeus (Fig. 4A–C). Such a setation of the head is an apomorphic character of the members of the so-called *C. abbreviatus*-complex (Mauss 2013). Pollen grains are removed from the anthers with the aid of these "knobbed" setae and accumulate between them on the front of the head. Then the pollen grains are transported towards the mouthparts with the fore legs, which bear comb-like rows of specialized, particularly strong pollen-brushing setae along the anterior margins of the inner surface of the first and the second segment of the fore tarsi (Fig. 4D–F). Pollen grains that occasionally accumulate on other parts of the body, particularly on the dorsal mesosoma and metasomal terga, are also transferred towards the mouthparts with the help of these "combs" on the fore tarsi.

It is of note that the spherically swollen ends of the "knobbed" setae look somewhat flattened and often concave from one side in the SEM images (Fig. 4C). Such depressions on the spherical distal ends of the setae were not reported for *C. abbreviatus* (Schremmer 1959; Müller 1996) but were present in all four specimens of both species in our study and are also visible in some original SEM images provided by A. Müller from his investigation of *C. abbreviatus* published in 1996. These depressions may be artifacts resulting from air-drying, in which the original spherical shape of the swollen ends of the setae seems to collapse partially.

**Male behaviour.** Males of *Celonites tauricus* were mainly observed at the site with flowering *Ziziphora taurica*, where they patrolled in flight along the plants or visited flowers. During flower visits they always inserted their proboscis into the corolla tube indicating the uptake of nectar. After that, they often performed pollen-brushing behaviour in the course of which the pollen grains were transferred from the frons towards the mouthparts, indicating pollen consumption as well (Fig. 3C). Patrolling males pounced on females that were visiting flowers or standing on the ground. Successful copulation was observed five times: four times on flowers (Fig. 3D, E) and one time on the ground (Fig. 3F). Each time, the whole copulation lasted less than 10 s, which is similar to the documented copulation length in two other previously studied species of *Celonites*, namely *C. abbreviatus* (Mauss 2006) and *C. fischeri* Spinola, 1838 (Mauss and Müller 2014).

## Conclusions

New records of *Celonites tauricus* from Dagestan, Georgia, and the main portion of Azerbaijan fill the gaps in its known distribution. The occurrence of the species in these areas was to be expected, since it was already known from neighbouring regions such as Armenia, Nakhchivan Autonomous Republic of Azerbaijan, and Northern Iran. The same is true for the records from Chios, Rhodes, and Samos. New data on forage plants and the flower-visiting behaviour of the wasps enlarge our bionomical knowledge of this species. The reported data confirm that *C. tauricus* is broadly oligolectic (*sensu* Müller and Kuhlmann 2008) exclusively visiting Lamiaceae. Moreover,

the observations point to a certain plasticity of the foraging behaviour of the females, which enables them to exploit the floral resources of a relatively broad range of various nototribic flowers of Lamiaceae as long as they fit in with their body proportions and pollen-collecting structures.

Oligolecty of variable degree seems to be typical of the genus *Celonites* Latreille, 1802. It was particularly confirmed to exist in other Palaearctic species visiting nototribic flowers of Lamiaceae that also use specialized pollen-collecting setae for pollen uptake from the anthers. From these species *Celonites abbreviatus*, which is closely related to *C. tauricus*, is evidently broadly oligolectic (Mauss 2006), while the just distantly related *Celonites sibiricus* has been recorded only on flowers of a single plant genus and thus can be treated as presumably narrowly oligolectic (Fateryga 2020). Species adapted to the pollen uptake from flowers of Boraginaceae with narrow corolla tubes, e.g., *Celonites heliotropii* Gess, 2007 from Namibia (Gess 2007; Gess and Gess 2010), *Celonites ivanovi* Mauss & Fateryga, 2022 from the Caucasus and *Celonites cagrii* Mauss & Yildirim, 2022 from east Anatolia (Mauss et al. 2022) are presumably also narrowly oligolectic, visiting exclusively flowers of plants belonging to the genus *Heliotropium* Tourn. ex L.

Most Afrotropical species of *Celonites* are broadly oligolectic visiting only a few closely related genera of either Scrophulariaceae or Campanulaceae (rarely Asteraceae in the case of *Celonites wheeleri* Brauns, 1905) but they are lacking specialized pollen-collecting structures and consume pollen directly from the anthers (Gess and Gess 1989, 2010). *Celonites capensis* Brauns, 1905 is, however, a clearly polylectic species visiting flowers of Asteraceae, Geraniaceae, Aizoaceae, Boraginaceae, Campanulaceae, Scrophulariaceae, and Iridaceae. These records indicate a certain plasticity of its behaviour. Another Afrotropical species, *Celonites promontorii* Brauns, 1905, collects pollen principally from Asteraceae but has been also recorded on flowers of two other plant families (Gess and Gess 1989, 2010). A few Palaearctic species that consume pollen directly from the anthers are known as narrowly oligolectic. These are *Celonites fischeri*, which is restricted to flowers of *Echium* Tourn. ex L. (Boraginaceae with broad corolla tubes) (Mauss and Müller 2014), and *Celonites kozlovi* Kostylev, 1935 that has been exclusively observed to collect pollen from nototribic flowers of *Dracocephalum* (Lamiaceae) but visits also several genera of Asteraceae for nectar uptake (Fateryga 2020). However, the narrow oligolecty of *C. kozlovi*, should be proofed in more detail, because it is not correlated with any specialized pollen-collecting structures present in other species of the genus that are adopted to pollen uptake from nototribic anthers. Finally, the presented data suggest that the trophic relationships of the genus *Celonites* with the angiosperm plants are still insufficiently studied (especially in the Palaearctic region) and that more field data are necessary to improve our knowledge on the ethology of these wasps.

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